

A NEW RHADOPLEURID HEMICHORDATE FROM THE MIDDLE CAMBRIAN OF SIBERIA

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ABSTRACT. *Rhabdopleura obuti* sp. nov. is described from the late Middle Cambrian Mayan Stage of the Sukhan Depression, Siberia, and is the second rhabdopleurid to be described from the Cambrian. It is probably one of the oldest 'living fossils', remaining unchanged for over 520 Ma. This colonial pterobranch consists of stolonial and zooidal tubes. The creeping portion commonly found in most pterobranchs is reduced, with the colony adopting an erect growth habit. The stolonial tubes frequently show dichotomies and contain stolons. It is the earliest record of stolons. The zooidal tubes widen distally and occasionally show branchings to form other zooidal tubes. Fuselli are common and possess a very irregular zig-zag suture. There is no thecal dimorphism. There are several dark bodies occurring within the zooidal tube which have been interpreted as dormant buds and zooidal material. The best preserved zooid occurs in an open-ended tube and is cigar shaped (0.7 by 0.2 mm) and attached proximally to a stolon. This is the earliest record of zooid material. A review of hemichordate zooids in the fossil record is presented. *Rhabdopleura obuti* is compared with other pterobranchs and graptolites, with the conclusion that it represents an early rhabdopleurid but has characters which represent the start of the graptolite evolutionary story.

THE close phylogenetic relationship between the pterobranchs and the graptolites, which was first suggested by Schepotieff (1905) and substantiated through the work of Kozłowski (1938, 1949*a*), is now well established from a variety of morphological, ultrastructural and chemical evidence (summarized by Rickards and Dumican 1984; Urbanek 1986). Predictions based on this close phylogenetic relationship suggest the occurrence of pterobranch-like ancestors in the Cambrian (Andres 1977, p. 89; Rickards 1979; Rickards *et al.* 1984). Attention has been focused on the early graptolite and pterobranch record in order to untangle the early evolution of these groups. The record of Middle Cambrian graptolites has developed over the last eighty years (North America: Ruedemann 1908, 1931, 1947; Australia: Chapman 1919; Chapman and Thomas 1936; Quilty 1971; Europe: Szűcs 1974) with a substantial Siberian component (Obut 1964, 1974). Middle Cambrian graptolite material further suggests an early occurrence of pterobranchs. The discovery of *Rhabdopleura* at this stratigraphical level will have great bearing in the study of the evolution of the pterobranchs and their relationship with the Graptolithina. A detailed study involving a phylogenetic classification of these groups and the origin and early evolution of the graptolites is currently being prepared for publication (by P. N. D.).

The material consists of a number of well-preserved, semi-transparent tubular colonial fossils with fusellar structures and sclerotized stolons constituting the earliest record of preserved stolon material. The fossils occur in a light-grey bedded limestone which can be easily prepared with acids. It is the earliest Cambrian pterobranch material to have been found in Siberia. It also represents a group which has remained unchanged for over 500 million years and is probably one of the oldest 'living fossils' (see below for discussion).

The only other record of a pterobranch from the Middle Cambrian is *Rhabdotubus johanssoni* Bengtson and Urbanek, 1986, from southern Sweden and Norway (see also Öpik 1933). The material described here was discovered in the collections of A. M. Obut at the Institute of Geology and Geophysics, Academy of Sciences, Novosibirsk during a visit made by Durman. It had been collected by K. S. Ziburid in 1957 (Field specimen No. 1738B) from a locality on the River Ukukit which is a western tributary from the middle region of the Rover Olenek, on the western flank of the Sukhan Depression. This is part of the Olenek structural region in the Yudoma–Olenek facies

region of the Siberian Platform (Kobanjikov 1959), in the Zelenotsvetnaya Formation. In modern usage this formation correlates with the Djahtaz and Siligir horizons from the Mayan Stage of the late Middle Cambrian (Shabanov *et al.* 1983). *Rhabdotubus johanssoni* is from the *Eccaparadoxides pinus* Biozone of the early Middle Cambrian, the earliest record of a pterobranch.

SYSTEMATIC PALAEOLOGY

Phylum HEMICHORDATA Bateson, 1885
 Class PTEROBRANCHIA Lankester, 1877
 Order RHABDOPLEURIDA Fowler, 1892
 Family RHABDOPLEURIDAE Harmer, 1905
 Genus RHABDOPLEURA Allman, 1869

Type species. *R. normani* Allman 1869a, p. 311 (see also Allman 1869b, p. 439; Allman 1869c, p. 58, pl. 8); Recent, from the Shetland Sea, Scotland, at 90 fathoms.

Rhabdopleura obuti sp. nov.

Plate 1, figs 1–4; Plate 2, figs 1–6; Text-figs 1–4

Derivation of name. After the Soviet graptolite worker Professor A. M. Obut who described much of the Siberian Cambrian graptolite material.

Material. The specimens are on five pieces of rock of which two fragments are housed at the Palaeontological Department of the Central Siberian Geological Museum in the Institute of Geology and Geophysics, Novosibirsk; registration number IGiG No. 962. Three other pieces of rock are deposited at the Sedgwick Museum, Cambridge (SM X.23262–23264).

Holotype. IGiG No. 962.

Paratypes. SM X.23262–23264.

Horizon and locality. Zelenotsvetnaya Formation, late Middle Cambrian, River Ukukit, Siberia.

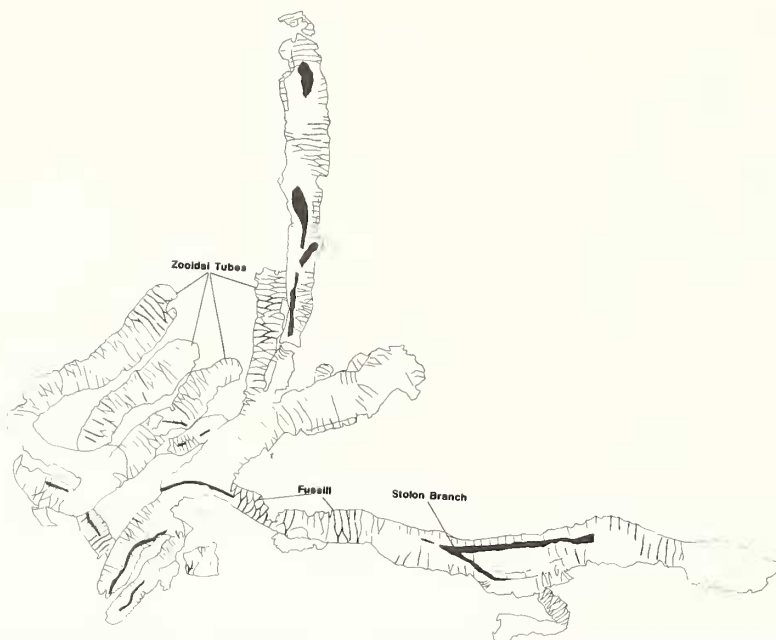
Associated species. *Siberiodendrum robustum* Obut, 1964 and *Archaeolafoea* sp. are in the same collection made by V. Ya Kobanjikov from this locality (housed at IGiG).

Diagnosis. Coenocium consisting of stolonial and zooidal tubes. Colony habitus largely erect with limited, encrusting, proximal portion. Stolonial tubes are 0.25–0.75 mm wide with irregular branchings. Sclerotized stolons common showing bifurcation at branch nodes. Stolon thickness between 60 and 80 μ m. The erect zooidal tubes are 6.6 mm long on average widening gradually to an aperture of about 1 mm. Branching of zooidal tubes occurs quite commonly. No thecal dimorphism or indication of cortical bandaging. Fusellar structures found throughout the whole colony with traces of very irregular zig-zag sutures in the stolonial tubes. Fusellar heights vary

EXPLANATION OF PLATE 1

Figs 1–4. *Rhabdopleura obuti* sp. nov. Zelenotsvetnaya Formation of the Mayan Stage, Middle Cambrian; River Ukukit (western tributary of River Olenek), Siberia. 1, IGiG No. 962, holotype; showing overall colony form with stolonial and zooidal tubes, fuselli and stolons visible, $\times 10$. 2, SM X.23264; possible coiled thecorhiza, $\times 16.6$. 3, SM X.23264; zooid in place within tube showing proximal stolon attachment, $\times 4.8$. 4, SM X.23264; zooid within tube with distal lophophore structure and proximal attachment point for stolon, $\times 4.8$.





TEXT-FIG. 1. Camera lucida drawing of the holotype of *Rhabdopleura obtusi* sp. nov. (IGiG No. 962) illustrating the overall colony form with fusellar structures and stolons. Dark bodies represent probable zooids or dormant buds, $\times 7$.

75–150 μm in stolonal tubes and 50–100 μm in zooidal tubes. Buds and zooids preserved within the tubarium with zooids measuring about 0.2 by 0.7 mm.

Description

Coenocium. The material consists of several distinct semi-transparent rhabdosomes and a number of isolated zooidal tubes (Plates 1–2; Text-figs 1–2). The overall colony form, such as any division into repent and erect tubes, is difficult to discern because the rhabdosomes have been flattened on burial. This flattening has also caused tubes to overlie one another and occur in a closer proximity to each other than they would have in life. The holotype has twelve distinct tubes and measures 12 by 9 mm (Pl. 1, fig. 1; Text-fig. 1). The upright zooidal tubes are the most common.

Stolonal tubes. The primary tubes have diameters of about 0.25–0.75 mm and are often seen with the better preserved stolon material (Pl. 2, figs 2, 5–6). The flattened tube diameters of 2.5 mm are associated with the very proximal tube portions nearest to the dichotomies. One tube fragment displays an area devoid of fuselli, running longitudinally down one side of the tube (Pl. 2, fig. 1). It has been interpreted as the structureless lower layer that occurs typically on the lower side of the creeping tubes in *Rhabdopleura* and also in some graptolites, for example the crustoids (Kozłowski 1962; Urbanek 1986). One specimen (Pl. 1, fig. 2) appears to be a coiled creeping tube forming a typical thecorhiza. No indication could be found in any of the material for any form of diaphragm or transverse structures which are found in Recent *Rhabdopleura*.

Zooidal tubes. The erect zooidal tubes arise by lateral branching from the primary stolonal tubes (Pl. 1, fig. 1; Pl. 2, fig. 2) and appear at a variety of orientations from the primary tube; they tend to form a lateral branch which twists around the main axis so that they run parallel to it, or can bend outwards at angles of up to 90°. The porus in the primary tube (where a zooidal tube emerges) is of the same diameter as the initial portion of the zooidal tube; branching apparently occurred by perforatory budding. The zooidal tubes vary in size: the longest complete tube is 8.5 mm (on the holotype); an average tube length is 6.6 mm ($n = 22$ complete tubes). The tubes are generally parallel sided or display a slight widening towards the aperture (Pl. 2, fig. 3). The diameter increase is about 0.5 mm over an average tube length, often with a greater expansion at the very

terminal portion giving rise to a funnel-shaped aperture (Pl. 2, fig. 3). The apertures of the tubes range from 0.47 to 1.25 mm in diameter (average about 0.87 mm; $n = 31$). Aperture ornamentation is not apparent but there is the possibility in some of the material that the apertures may have an oblique margin at an angle of 20°–30° to the edge of the tube; however, this may be a taphonomic affect. These variations described are probably due to preservational or local growth differences rather than any form of thecal dimorphism. The coenocia of the zooidal tubes are often darker more proximally and become lighter distally, a feature related to secondary thickening which is more prevalent proximally or to greater proximal sclerotization.

Fusellar structure. Full fusellar rings are most prevalent; rarer half-rings occur most frequently proximally and in the stolonal portions. The zig-zag suture is very indistinct and irregular but can be seen over short lengths (Pl. 2, fig. 2; cf. *Rhabdopleura kozłowskii* Kulicki, 1969). Zooidal tubes mainly comprise complete fusellar rings with an oblique suture which is often irregularly placed as in the case of most rhabdopleurids and some graptolites. The distal parts of the fuselli frequently protrude to give the appearance of a collar which is very characteristic of the rhabdopleurid fusellar arrangement (Pl. 2, fig. 5). The height of the fuselli (i.e. the distance between the growth lines) varies with position in the colony: the stolonal tubes have fusellar heights in the range 75–150 μm , the zooidal tube fuselli 50–100 μm . Thus over a 2.5 mm portion, the stolonal tubes have about 18–22 fuselli compared with 25–35 fuselli in zooidal tubes.

Stolons. The stolons are very common throughout the colonies and more frequent in the repent tubes. The stolons appear as dark rods often with relief. Their common occurrence is due to the sclerotization which toughens the material and makes their preservation potential greater. The longest stolon is 6.38 mm with a thickness of 60 μm ; stolon thickness ranges from 60 to 80 μm . The stolons frequently appear to bifurcate at the lateral branches (Text-fig. 1). The stolons swell at these nodes (Pl. 2, figs 2, 5–6).

Buds and zooids. At a number of places, there are dark bodies which may be interpreted as dormant buds or zooids. However, it is possible to confuse areas of tube overlap with these zooids as they both appear darker than the surrounding region and care must be taken in the interpretation. The clearest example of a preserved zooid occurs in an open-ended tube; it is cigar shaped, measuring 0.7 mm long by 0.2 mm wide (Pl. 1, fig. 3; Text-fig. 3). It is attached proximally to a 67 μm wide stolon and is preserved in three dimensions but no further anatomical details can be seen. In one specimen (SM X.23264; Pl. 1, fig. 4) there is a suggestion of a lophophore. At the distal end of the zooid in SM X.23262 there is a small projection which may be remnants of the pre-oral disc or cephalic shield (Pl. 1, fig. 3). The size compares well with accounts of Recent rhabdopleuran zooids which measure <0.5–1.0 mm (Bulman 1970; Stebbing 1970) and with the unique record of graptolite zooids recorded as being 'rather less than half a millimetre' (Rickards and Stait 1984).

Discussion. The general appearance of the coenocium with the proximal semi-annular fuselli and zooidal tubes displaying irregular, annular fuselli is in itself sufficient to place these specimens in *Rhabdopleura*; the occurrence of sclerotized stolon and zooidal bodies makes this placement conclusive. Other features, such as the development of the secondary thickening in the proximal areas, are common in *Rhabdopleura normani*. The absence of thecal dimorphism prevents inclusion in the graptolites (as thecal dimorphism is essentially a graptolitic character secondarily lost in the graptoloids). The only character which is not properly accounted for within extant *Rhabdopleura* is the occurrence of distally widening tubes (although Andres has reported them in specimens from Bergen, Norway – see below). The proposal to erect a new genus or subgenus was considered at length (see later for comparison and discussion), but it was decided that the differences between the extant species were no greater than the differences between them and *R. obuti*, and the proposal was abandoned. There is a series of parallel-sided lines which run longitudinally in some of the tubes which look similar to cortical bandages. However, a number of the lines converge and cross which suggests that they are due to wrinkling from tube flattening; if they were cortical bandages, the lines would be expected to maintain a parallel relationship along their entire length. There is no indication of any type of solid substrate such as shell material, and presumably the good preservation indicates the colony has not been transported any great distance. Text-figure 4 illustrates the authors' concept of how the organism *Rhabdopleura obuti* might have appeared in life.

COMPARISON WITH OTHER PTEROBRANCHS AND GRAPTOLITES

Despite the simple morphology of the rhabdopleurids, their ecophenotypic variability has made classification confused in the past. Identification of extant species of *Rhabdopleura* has been much debated with great deal of synonymizing and species splitting (Thomas and Davies 1949a). This is mainly due to the very varied forms that the genus can adopt, related to substrate interaction. Fossil species have similarly undergone much discussion but this debate has often been at a higher taxonomic level and, due to Mierzejewski (1986), at the family level. Bulman (1970) was the first to place all the fossil pterobranchs into the family Rhabdopleuridae, as previous workers such as Kozłowski showed a reluctance to use families in classification. Mierzejewski (1986) adopted a different approach with the different fossil genera representing three families with three distinct phylogenetic lines.

Comparison with Recent Rhabdopleura

Seven Recent species of *Rhabdopleura* have been described; Thomas and Davies (1949a) gave an account of their classification and its problems. It was suggested by van der Horst (1936) that these seven species can be synonymized into three, based on a geographical distribution (*R. normani* – Atlantic; *R. striata* – Sri Lanka; and *R. annulata* – New Zealand, Celebes and Tasmania). This scheme has been adopted by most workers. *R. normani* is very variable with the zooidal tubes arising with poorly to well developed adherent portions (Lankester 1886, p. 625). *R. annulata* lacks an adherent portion but the creeping portion is well developed. *R. obuti* differs from most of the Recent examples of *Rhabdopleura* in lacking a distinct and significant creeping portion of the stolon tubes, with a very irregular and limited zig-zag suture in the stolon tubes which widen distally. However, there are rare examples of other rhabdopleurids demonstrating characters such as distally widening tubes, e.g. *Rhabdopleurites primaevus* Kozłowski, 1967 and Recent *Rhabdopleura* from Bergen, Norway (Dietmar Andres pers. comm.). Branching of the zooidal tubes is rare in Recent *Rhabdopleura* but has been reported (Schepotieff 1907, pls 17, 21; Kozłowski 1949a, fig. 14); Kulicki 1971, fig. 2G–H). It is rarely seen in *R. normani* (Noel Dilly pers. comm.). The limited creeping portion of *Rhabdopleura obuti* is perhaps a reflection of the soft substrate on which it lived. Rhabdopleurids are usually found associated with hard substrates such as pebbles, corals, ascidians and shells, although *R. mirabilis* Sars, 1874 is reported to be attached to mud, sand particles, and associated foraminiferal tests. *R. normani* is known to grow on sand particles off the Faeroe Islands (Noel Dilly pers. comm.).

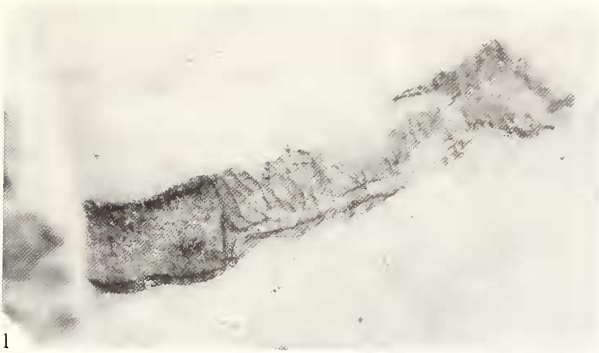
Comparison with fossil rhabdopleurids

Rhabdopleura eocenica Thomas and Davies, 1949b (Yprésian, Eocene, Lower Swanwick, Hampshire); *R. vistulae* Kozłowski, 1949b (Upper Cretaceous, Poland); *R. dehneri* Mortelmans, 1955 (Viséan, Turnhout, Belgium); *R. kozłowskii* Kulicki, 1969 (Bathonian, southern Poland); *R.?* sp. Mierzejewski, 1978 (Ludlow, Silurian, Poland) and *R. hollandi* Rickards *et al.*, 1984 (Upper Llandovery, Powys, Wales) all display features very much like Recent *Rhabdopleura*. *R. obuti* is very comparable with these forms and only differs from them in the characters listed above.

Many of the rhabdopleurids described by Kozłowski (*Rhabdopleuroides expectatus* Kozłowski,

EXPLANATION OF PLATE 2

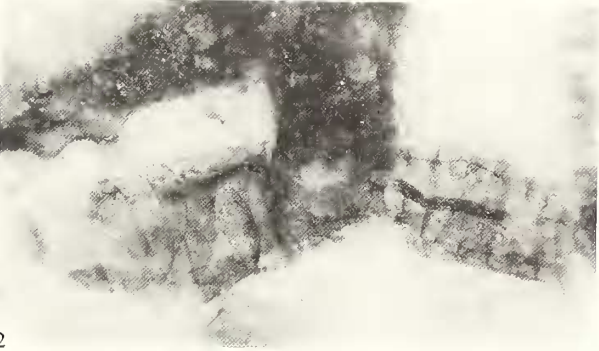
Figs 1–6. *Rhabdopleura obuti* sp. nov. Zelenotsvetnaya Formation of the Mayan Stage, Middle Cambrian; River Ukukit (western tributary of Rover Olenek), Siberia. 1, SM X.23263; stolon tube illustrating structureless lower layer, $\times 17.5$. 2, SM X.23262; stolon tube with branch, fuselli and stolons, $\times 35$. 3, SM X.23264; typical zooidal tube with funnel-shaped aperture and fuselli, $\times 14.2$. 4, SM X.23264; collection of branching zooidal tubes, $\times 3.7$. 5, SM X.23262; stolon tube with stolon and collar-shaped fuselli, $\times 40$. 6, SM, X.23262; stolon tube with branching stolon, $\times 17.7$.



1



3



2



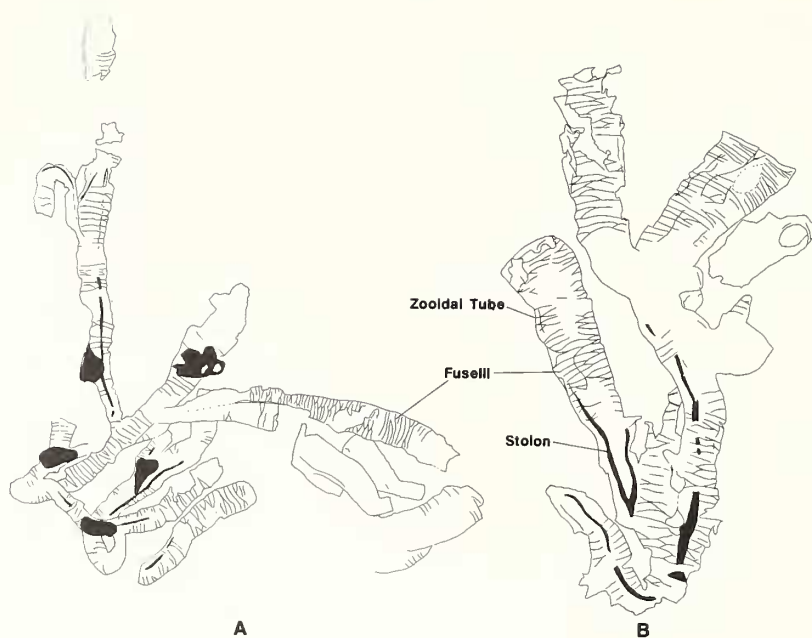
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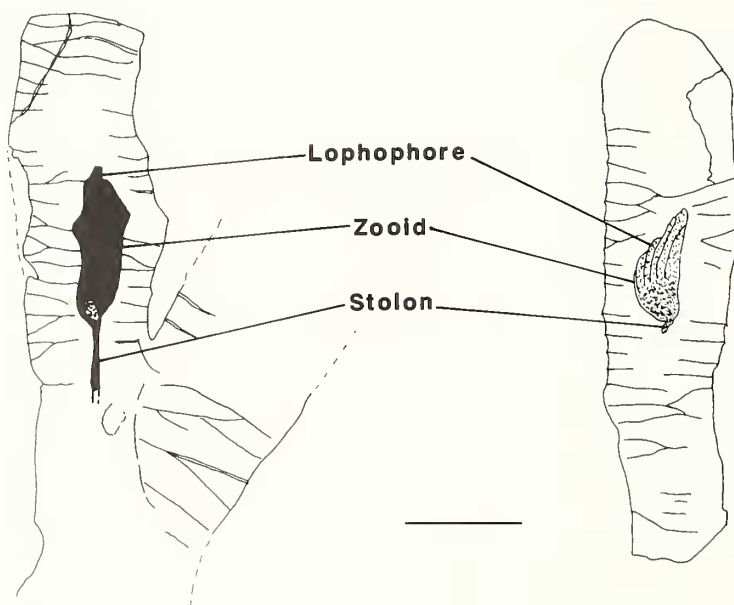
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6



TEXT-FIG. 2. *Rhabdopleura obuti* sp. nov. showing overall colony arrangement. A, SM X.23262; large dark bodies are probable zooids, $\times 5$. B, SM X.23264; collection of branching zooidal tubes, $\times 2.5$.



TEXT-FIG. 3. Zooids belonging to *Rhabdopleura obuti* sp. nov. SM X.23264. Both zooids occur within zooidal tubes displaying fuselli and possibly exhibit lophophores distally and stolon structures proximally. Scale bar represents 0.5 mm.

1961 (Upper Ordovician, Poland); *Rhabdopleurites primaevus* Kozłowski, 1967 (Ordovician, Poland) and *Kystodendron* Kozłowski, 1959 (Ordovician, Poland)) appear to be very similar to Recent *Rhabdopleura*. However, they are differentiated on the basis of a few characters listed as follows: *R. expectatus* lacks dormant buds, possesses apertural languettes and the zooidal tubes are attached throughout their length; *R. primaevus* possesses non-fusellar portions, but the sterile buds are missing and it is based on very fragmentary material; and *Kystodendron* (includes *Eorhabdopleura* Kozłowski, 1970) has major stolons and peduncular stolons of cysts of sterile buds which lack diaphragms. We believe that these characters are not sufficient to define taxa separate from *Rhabdopleura*. The characters on which these taxa are defined are often absence characters which are not useful when dealing with fossil material. Clearly, the lack of a character may be simply related to its poor preservation. Additionally, Kozłowski's material was mainly derived from acid isolation techniques which have been useful in obtaining new material but can also cause damage to specimens.

The only other Middle Cambrian rhabdopleurid, *Rhabdotubus johaussoni* Bengtson and Urbanek, 1986 has a very similar appearance to the material described here. *Rhabdotubus* has tubes displaying creeping portions and zooidal tubes which widen distally, with very similar fusellar arrangements. There are lateral branches to the zooidal tubes and the colony sizes are very comparable. However the colonies of *Rhabdotubus* differ by having a more discrete basal structure and also the erect zooidal tubes occur frequently as adnate bundles. *Rhabdotubus* also seems to show a preference for firm substrates such as brachiopod valves, which may be the reason why there is a better developed thecorhiza. There is an absence of stolons or related structures in *Rhabdotubus*, which has been interpreted as a lack of stolon sclerotization (Bengtson and Urbanek 1986).

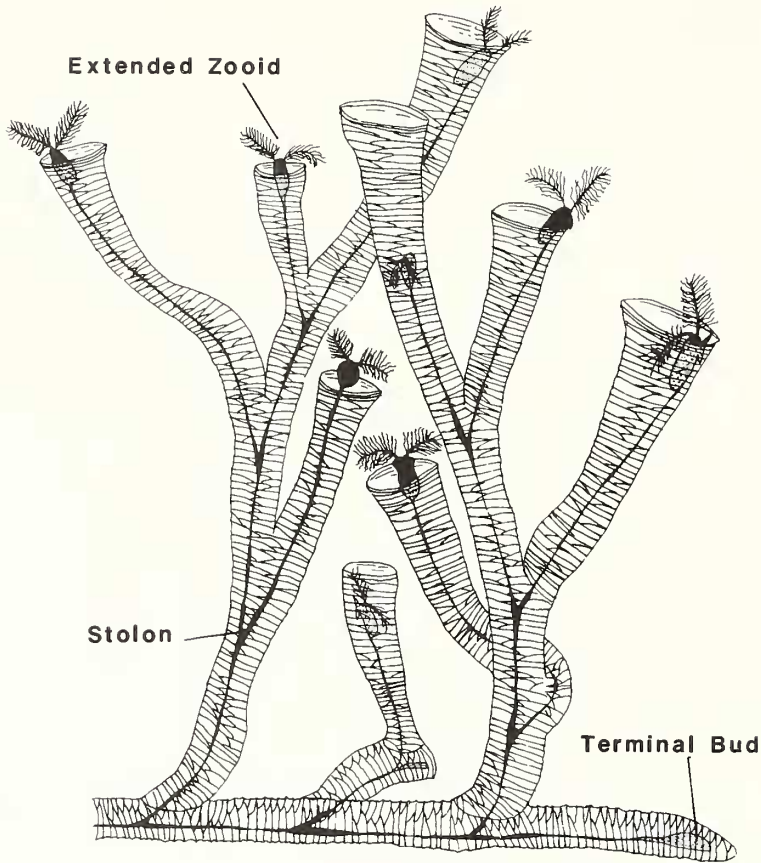
Bengtson and Urbanek (1986) proposed that *Rhabdotubus* is an intermediate form between the rhabdopleuran pterobranchs and the tuboid graptolites with a mosaic of characters from both groups. The main points of evidence that they have for the association with the tuboids are: the striking resemblance of the colony habitus; the occurrence of a ventral apertural lip; and the steady increase of the zooidal tube diameter and the lack of a sclerotized stolon system. *Rhabdopleura obuti* is probably more closely related to Recent rhabdopleurids than *Rhabdotubus*, but also shows some characters that are seen in the tuboid graptolites such as the distally widening tubes. These Middle Cambrian rhabdopleurans provide evidence for the divergence of the rhabdopleurid and tuboid groups which is an important phase of hemichordate evolution.

Comparison with Fasciculitubus Obut and Sobolevskaya, 1967

This genus is remarkably similar to *Rhabdotubus* and they are probably synonymous; however, for the present *Fasciculitubus* should merely be removed from the graptolite Idiotubidae to the pterobranch Rhabdopleuridae. It has a very comparable colony habitus with a distinct basal portion and erect cylindrical tubes. Urbanek (pers. comm.) agrees that *Rhabdotubus* and *Fasciculitubus* are very similar.

RHABDOPLEURA: A 'LIVING FOSSIL'

The discovery of rhabdopleurids at this stratigraphical level indicates the remarkably conservative nature of the group. The basic morphology has remained unchanged for 520 Ma, consisting of a series of creeping tubes with erect zooidal tubes and a branching system of sclerotized stolons. This represents one of the oldest 'living fossils', characterized by a low species diversity and a set of morphological traits which persist over an extraordinarily long time range. The existence of 'living fossils' has been considered paradoxical in the sense that changing environments over such a long period would surely have prompted some form of evolutionary change. 'Living fossils' have been considered in terms of rates of evolution. The two main explanations are that slow transformation, producing little anatomical diversity, accounts for low observed taxonomic diversity or, in reverse, that low rates of speciation have slowed the acquisition of morphological diversity (Eldredge 1984).



TEXT-FIG. 4. Reconstruction of *Rhabdopleura obuti* sp. nov. with branching zooidal tubes, bifurcating stolons, terminal bud and feeding zooids. The overall zooid morphology is taken from the preserved material and by comparison with Recent species. The zooids are mainly shown feeding at the tube rims. A dormant bud at the terminal portion is also indicated. The attached portion of the colony is somewhat reduced, with a dichotomizing system of zooidal tubes above. The zooidal tubes show the distally widening tubes with funnel-shaped apertures.

Our understanding of why *Rhabdopleura* is a 'living fossil' is hampered by a limited knowledge of its geographical distribution through time, and the fragmentary fossil record. So, although it is difficult to explain the occurrence of *Rhabdopleura* in terms of evolutionary rates, it is somewhat easier to speculate how this organism has succeeded to defy extinction.

Recent *Rhabdopleura* is commonly found inhabiting cryptic environments such as on the concave surface of bivalve shells. During a dredging study off Stoke Point, Plymouth, 61 per cent of the colonies were found on this inner surface of shells such as *Glycimeris glycimeris* (Stebbing 1970). Observations of colonies in life position at the same locality (by SCUBA diving) revealed that the dead shells were in abundance, and all the separated valves were lying concave side downwards. The specificity of habitat is likely to be related to selection by the larvae on settling, enabled by its mobility, but its exact mode is unknown (Dilly 1973). Other cryptic environments have been utilized such as dead serpulid tubes, in the holes left by the sponge, *Cliona celata*, or in the burrows of boring polychaetes (Stebbing 1970). The cryptic nature of the habitat is clearly advantageous with respect to avoiding predation, adverse conditions etc. and, although *Glycimeris* has not existed as long as

Rhabdopleura, there were presumably other suitable host shells during earlier times, such as trilobite moults. 'Living fossils' are often seen to inhabit restricted environments; for example, *Nautilus* lives in deep, fore-reef slope environments. It is thought that *Nautilus* retreated to deeper waters (facilitated by the ability to survive in low-oxygen conditions) to avoid competition with the newly evolved fast-moving fish (Wells *et al.* 1992). Similarly, representatives of the Pleurotomariidae (Gastropoda) are widely known from the Cambrian, but today they are only known from deep water environments (> 200 m), of low latitudes and hard substrates (Hickman 1984). These groups have been known from much broader environments in the geological past but today are restricted to *refugia*-type environments.

Another factor which may have favoured their survival is the ability to overwinter by encystment. Recent *Rhabdopleura* produce buds consisting of a spherical or ovoid mass of yolky globules which are sometimes enclosed in a darkly pigmented case (Dilly 1975). These have been variously referred to as hibernacula (Lankester 1884), sterile buds (Schepotieff 1907) or dormant buds (Stebbing 1970). There are commonly several dormant buds in each colony. They are formed from the base of the contractile stalks of adult zooids and became separated from them into a chamber in the repeat coenocium by the secretion of a septum across the tube. The material composing the dormant bud wall (which is very similar to graptolite periderm) is clearly very resistant as it is commonly preserved in the fossil record. This resulting yolk store is contributed by many of the zooids in the colony, but it is not clear as to whether this food supply is generally available in times of shortage. It is perhaps more likely that the colony dies back in the winter and that fresh zooids develop from dark cells surrounding the yolk within the bud (Dilly 1975). This adaptation to overwintering has enabled the group to survive through periods of low food levels and other adverse conditions. It is not known how resistant these dormant buds are; perhaps they could survive for several years to produce viable colonies. The acquisition of the dormant buds occurred early in the phylogeny of the group, as it has been proposed that the graptoblasts, associated with the crustoid graptolites, represent structures homologous to dormant buds (Urbanek 1983). Graptoblasts are found as early as the Lower Ordovician. Dormant buds are not found in any of the other Hemichordata; they first appeared in the pterobranchs and were subsequently lost at some point during the evolution of the graptolites (Durman unpublished). Their occurrence in the rhabdopleurids could have been a significant factor for the survival of the group through mass extinctions.

The simple morphology of the rhabdopleurids has allowed substantial ecophenotypic variation enabling adaptation to changing environments. This has been assisted further through its modular development of its colonial habit allowing variability within the colony. The reproductive strategies have also been an aid to its survival. *Rhabdopleura* is able to reproduce sexually (probably during more favourable times) and can bud asexually as part of the growth of the colony and reproduction (during less favourable times). The exact bathymetric range of *Rhabdopleura* is unknown but *R. normani* tends to be a relatively deep water form with *R. compacta* occurring in comparatively shallower waters (Plymouth Sound and the coast of Bermuda, respectively). Although it is most commonly found in cryptic environments, it has also been reported from coarse sandy substrates and even mud. *Rhabdopleura* appears to have quite a wide tolerance of physical conditions, but seems to select cryptic environments over non-cryptic. A combination of the cryptic life habit, a persistent life-cycle strategy and adaptability has allowed the survival of this remarkable genus to the present day.

HEMICHORDATE ZOOIDS IN THE FOSSIL RECORD

The first account of zooids in the fossil record was by Rickards and Stait (1984; see also Rickards *et al.* 1991) where several zooids were found in the thecae of *Psigraptus jacksoni* (Tremadoc); they are pyritized and preserved in three dimensions. Previous to these accounts, deductions about the size and function of zooids had to be made by comparison with living pterobranchs and by analysis of the structures these zooids made, i.e. the fuselli and cortical bandages of the rhabdosomes (Crowther and Rickards 1977). A recent paper by Sudbury (1991) proposed a formula for the size

of the zooid based on its relationship with fusellus height (FH), that is, the graptolite zooid would be 1.5 FH wide and 4.5 FH long. It is quite likely that such a relationship exists as the fuselli are structures secreted by the cephalic shield of the zooid. The discovery of preserved zooid material associated with *Rhabdopleura obuti* is an ideal opportunity to test some of these ideas (Pl. 1, figs 3–4; Text-fig. 3). Measurements of the fusellar heights from a tube containing a zooid range from 67 to 84 μm and average 75 μm . If the formula is applied to these measurements, a zooid measuring 113 μm wide by 338 μm long would be expected to have built the tube. The zooid within the tube measures 200 by 700 μm , about double the dimensions predicted by the formula. If one assumes that the formula is accurate, the measurements represent the size of the zooid that built the tube, suggesting that the zooid has doubled in size following its completion. This increase in size could be related to a change in life functions such as sexual reproduction. Sudbury (1991, p. 384) mentioned that the graptolite zooids of her study appear to produce over large thecae and, she proposed that the tubes were built rapidly and that the construction of fuselli was part of the earlier stages of the ontogeny. After the tube was complete the zooid could then embark on the final stage of its ontogeny, including the production of gonads for sexual reproduction, causing a further increase in zooid size. The measurements here concur with Sudbury's predictions.

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REFERENCES

- ALLMAN, G. J. 1869a. *Rhabdopleura normani*, Allman, nov. gen. et sp. *Report of the British Association for the Advancement of Science*, for 1868, 311–312.
- 1869b. On *Rhabdopleura*, a new genus of Polyzoa. *Proceedings of the Royal Society of Edinburgh*, **6**, 438–440.
- 1869c. On *Rhabdopleura*, a new form of Polyzoa, from deep-sea dredging in Shetland. *Quarterly Journal of Microscopical Science, London*, **9**, 57–63.
- ANDRES, D. 1977. Graptolithen aus ordovizischen Geschieben und die frühe Stammesgeschichte der Graptolithen. *Paläontologische Zeitschrift*, **51**, 52–93.
- BATESON, W. 1885. The later stages in the development of *Balanoglossus kowalevsi*, with a suggestion as to the affinities of the Enteropneusta. *Quarterly Journal of Microscopical Science, London*, **25** (Supplement), 81–122, pls 4–9.
- BENGTSON, S. and URBANEK, A. 1986. *Rhabdotubus*, a Middle Cambrian rhabdopleurid hemichordate. *Lethaia*, **19**, 293–308.
- BULMAN, O. M. B. 1970. Graptolithina, with sections on Enteropneusta and Pterobranchia. VI–V163. In TEICHERT, C. (ed.). *Treatise on invertebrate paleontology. Part V*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, xxxii + 163 pp.
- CHAPMAN, F. 1919. On some hydroid remains of Lower Palaeozoic age from Monegeeta, near Lancefield. *Proceedings of the Royal Society of Victoria*, **31**, 388–393, pls 19–20.
- and THOMAS, D. E. 1936. The Cambrian Hydroida of the Heathcote and Monegeeta Districts. *Proceedings of the Royal Society of Victoria*, **48**, 193–212, pls 14–17.
- CROWTHER, P. and RICKARDS, R. B. 1977. Cortical bandages and the graptolite zooid. *Geologica et Palaeontologica*, **11**, 9–46.
- DILLY, P. N. 1973. The larva of *Rhabdopleura compacta* (Hemichordata). *Marine Biology*, **18**, 69–86.
- 1975. The dormant buds of *Rhabdopleura compacta* (Hemichordata). *Cell and Tissue Research*, **159**, 387–397.
- ELDREDGE, N. 1984. Simpson's inverse: Bradytely and the phenomenon of 'living fossils'. 272–277. In ELDREDGE, N. and STANLEY, S. M. (eds). *Living fossils*. Springer-Verlag, New York, 291 pp.

- FOWLER, G. H. 1892. The morphology of *Rhabdopleura allmani*. 293–297. In LEUCKARTS, R. (ed.). *Festschrift zum 70ten Geburtstag*. W. Engelmann, Leipzig, 413 pp.
- HARMER, S. F. 1905. The Pterobranchia of the Siboga-Expedition with an account of other species. 1–102. In WEBER, M. (ed.). *Résultats des explorations à bord du Siboga, Monographie*. 26 bis. E. J. Brill, Leiden, 132 pp.
- HICKMAN, C. S. 1984. *Plenrotomaria*: pedigreed perseverance. 225–231. In ELDREDGE, N. and STANLEY, S. M. (eds). *Living fossils*. Springer-Verlag, New York, 291 pp.
- HORST, C. J. VAN DER 1936. Pterobranchia. 534–539. In BRONN, H. H. (ed.). *Klassen und Ordnung des Tier-Reichs*. Vol. 4, Abt. 4, Buch 2, T. 2. Akademische Verlagsgesellschaft m. b. H., Leipzig, 737 pp.
- KOBANJIKOV, V. YA. 1959. Yugo-vostochnuy sklon Anabarskog podnatiya – Sukhansky progib. Stratigraphiya siniiyskyh i kembriyskyh otlozheny severovostoka Sibirskoy Platformy. *Trudy Nauchno-issledovatel' Skogo Instituta Geologii Arktiki*, 101, 68–81. [In Russian].
- KOZLOWSKI, R. 1938. Informations préliminaires sur les Graptolithes du Tremadoc de la Pologne et sur leur portée théorique. *Annales Musei Zoologici Polonici*, 13, 183–196.
- 1949a. Les graptolithes et quelques nouveaux groupes d'animaux du Tremadoc de la Pologne. *Acta Palaeontologica Polonica*, 3, 1–235.
- 1949b. Découverte du Pterobranchie *Rhabdopleura* à l'état fossile dans le Crétacé supérieur en Pologne. *Compte Rendu de l'Académie des Sciences, Paris*, 228, 1505–1507.
- 1959. Les hydroides ordoviciens à squelette chitineux. *Acta Palaeontologica Polonica*, 4, 209–271.
- 1961. Découverte d'un rhabdopleuride (Pterobranchia) Ordovicien. *Acta Palaeontologica Polonica*, 6, 3–16.
- 1962. Crustoidea – nouveau group de graptolites. *Acta Palaeontologica Polonica*, 7, 3–52.
- 1967. Sur certains fossiles Ordoviciens à test organique. *Acta Palaeontologica Polonica*, 12, 99–132.
- 1970. Nouvelles observations sur les rhabdopleurides (Pterobranchies) Ordovicien. *Acta Palaeontologica Polonica*, 15, 3–17.
- KULICKI, C. 1969. The discovery of *Rhabdopleura* (Pterobranchia) in the Jurassic of Poland. *Acta Palaeontologica Polonica*, 14, 537–551.
- LANKESTER, E. R. 1877. Notes on the embryology and classification of the animal kingdom: comprising a revision of speculations relative to the origin and significance of germ layers. *Quarterly Journal of Microscopical Science, London*, 17, 399–454.
- 1884. A contribution to the knowledge of *Rhabdopleura*. *Quarterly Journal of Microscopical Science, London*, 24, 622–647.
- MIERZEJEWSKI, P. 1978. The first discovery of Crustoidea (Graptolithina) and Rhabdopleurida (Pterobranchia) in the Silurian. *Bulletin de l'Académie Polonaise des Sciences. Série des Sciences de la Terre*, 25, 103–107.
- 1986. Ultrastructure, taxonomy and affinities of some Ordovician and Silurian microfossils. *Palaeontologia Polonica*, 47, 129–220.
- MORTELMANS, G. 1955. Découverte d'un Pterobranchie, *Rhabdopleura delmeri* nov. sp., dans le viséan terminal du sondage de Turnhout. *Bulletin de la Société Belge de Géologie*, 64, 52–66.
- OBUT, A. M. 1964. [Order Hemichordata]. 279–337. In ORLOV, Y. A. (ed.). *Osnovy Palaeontologii*. Nedra Press, Moscow, 383 pp. [In Russian].
- 1974. New graptolites from the Middle Cambrian of the Siberian Platform. *Special Papers in Palaeontology*, 13, 9–13.
- and SOBOLEVSKAYA, R. F. 1967. *Nekotornye stereostolonata pozdnego kembriya i ordovika Noriljskogo rayona. Novye dannye po Biostratigrafii nizhnego paeozoya Sibirskoy Platformy*. Nauka, Moscow, pp. 45–64. [In Russian].
- ÖPIK, A. A. 1933. Über einen Kambrischen Graptolithen aus Norwegen. *Norsk Geologisk Tidsskrift*, 13, 113–115.
- QUILTY, P. G. 1971. Cambrian and Ordovician dendroids and hydroids of Tasmania. *Journal of the Geological Society of Australia*, 17, 171–189.
- RICKARDS, R. B. 1979. Early evolution of graptolites and related groups. 435–441. In HOUSE, M. R. (ed.). *The origin of major invertebrate groups*. 1st ed. The Systematics Association Special Volume 12. Academic Press, London and New York, 515 pp.
- CHAPMAN, A. J. and TEMPLE, J. T. 1984. *Rhabdopleura hollandi*, a new pterobranch hemichordate from the Silurian of the Llandoverly district, Powys, Wales. *Proceedings of the Geologists' Association*, 95, 23–28.
- and DUMICAN, L. W. 1984. Graptolite ultrastructure; evolution of descriptive and conceptual terminology. *Geological Magazine*, 122, 125–137.
- PARTRIDGE, P. L. and BANKS, M. R. 1991. *Psigraptus jacksoni* Rickards and Stait – preservation, distribution and reconstruction. *Alcheringa*, 15, 243–254.

- and STAIT, B. A. 1984. *Psigraptus*, its classification, evolution and zooid. *Alcheringa*, **8**, 101–111.
- RUEDEMANN, R. 1908. Graptolites of New York. Part 2. Graptolites of the Higher Beds. *Memoir of the New York State Museum*, **11**, 1–583.
- 1931. Some new Middle Cambrian fossils from British Columbia. *Proceedings of the United States National Museum*, **79**, 1–18.
- 1947. Graptolites of North America. *Memoir of the Geological Society of America*, **19**, 1–652.
- SARS, G. O. 1874. On *Rhabdopleura mirabilis* (M. Sars). *Quarterly Journal of Microscopical Science, Loudon*, **14**, 23–44.
- SCHEPOTIEFF, A. 1905. Über die Stellung der Graptolithen im zoologischen System. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, for **1905**, 79–98.
- 1907. Die Pterobranchier. *Zoologische Jahrbücher*, **23**, 463–534.
- SDZUY, K. 1974. Mittelkambrische Graptolithen aus NW-Spanien. *Paläontologische Zeitschrift*, **48**, 110–139.
- SHABANOV, YU. YA., EGOROVA, L. I., SAVITSKY, V. E. and PEGEL, T. V. 1983. Regional'naya stratigraficheskaya schema srednekembrijskoy otlozheny Sibirskoy Platformy. Resheniya po dokembriya, paleozoyu i chetvertichnoy sisteme Sredney Sibiri. *Trudy Siborskogo Nauchno-issledovatel'Skogo Instituta Geologii, Geofiziki i Mineral'nogo Syr'ya*, 103–109. [In Russian].
- STEBBING, A. R. D. 1970. Aspects of the reproduction and the life-cycle of *Rhabdopleura compacta* (Hemichordata) from Plymouth. *Marine Biology*, **5**, 205–212.
- SUDBURY, M. 1991. The dimensions of the graptolite zooid. *Geological Magazine*, **128**, 381–384.
- THOMAS, H. D. and DAVIES, A. G. 1949a. The pterobranch *Rhabdopleura* in the English Eocene. *Bulletin of the British Museum (Natural History), Geology Series*, **1**, 1–24.
- 1949b. A fossil species of the pterobranch *Rhabdopleura*. *Abstracts of the Proceedings of the Geological Society, London*, **1450**, 79.
- URBANEK, A. 1983. The significance of graptoblasts in the life cycle of crustoid graptolites. *Acta Palaeontologica Polonica*, **28**, 313–326.
- 1986. The enigma of graptolite ancestry: lesson from a phylogenetic debate. 184–226. In HOFFMAN, A. and NITECKI, M. H. (eds). *Problematic fossil taxa*. Oxford Monographs on Geology and Geophysics, 5. Clarendon Press, Oxford, 267 pp.
- WELLS, M. J., WELLS, J. and O'DOR, R. K. 1992. Life at low oxygen tensions: the behaviour and physiology of *Nautilus pompilius* and the biology of extinct forms. *Journal of the Marine Biological Association of the United Kingdom*, **72**, 313–328.

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